1999

Alarm Calls Affect Foraging Behavior in Eastern Chipmunks (Tamias striatus)

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ALARM CALLS AFFECT FORAGING BEHAVIOR

IN EASTERN CHIPMUNKS (Tamias striatus)
(TITLE)

BY

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1973-

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1999
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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Abstract: I used playback experiments to test whether alarm calls affected the foraging behavior of Eastern chipmunks (*Tamias striatus*). I subjected chipmunks, foraging at artificial feeding stations, to three playback treatments (silent, control noise, and alarm call) and examined changes in vigilant and foraging behavior. Chipmunks responded to alarm calls with a greater degree and duration of vigilant behavior, such as look-ups and alert postures. Chipmunks also ran a shorter distance to cover, ran more directly to cover, and took longer to re-emerge from the burrow after hearing an alarm call. Alarm calls caused individuals to spend more time out at the feeding stations, however, these individuals took significantly fewer seeds after hearing an alarm call. This was not due to a difference in the time spent handling food, but rather a slower rate of loading. Chipmunks appear to sacrifice energy gain by increasing vigilance after hearing an alarm call. This study suggests that, to avoid the costs of unnecessary escape behavior, individuals directly assess their own risk rather than relying only on indirect cues such as alarm calls.

ACKNOWLEDGEMENTS

I thank Paul Switzer for his help with the design of the project and with the manuscript. I thank Eric Bollinger for his comments on the manuscript and Tom Nelson for assistance with trapping and marking and for his comments on the manuscript. Also, thanks to Dan Blumstein for his suggestions on the manuscript and throughout the study. Special thanks to Connie Huber, Andrew Methven, Kipp McGilliard, Susie Mounce, Britto Nathan and their respective families for the use of their property on which experiments were conducted.

Introduction:

Foraging often carries with it a danger of predation, which may alter considerably predictions of the classical optimal foraging models (Lima and Dill, 1990). We must, therefore, consider predation risk as well as food characteristics for animals that are predator and potential prey at the same time (Holmes, 1984). Predation risk is characterized by the probability of being encountered by and being attacked or killed by a predator (Newman et al., 1988; Lima and Dill, 1990), and may affect various components of foraging such as diet selection (Dill and Fraser, 1984; Lima and Valone, 1986; Phelan and Baker, 1992; Otter, 1994), habitat choice (Anderson, 1986; Gilliam and Fraser, 1987; Holmes, 1991; Hughes and Ward, 1993; Brown and Morgan, 1995), the distribution of competitors among resources (Newman and Caraco, 1987), and patch exploitation (Holmes, 1984; Lima et al., 1985). Animals face a trade-off in which they must balance two conflicting demands (energy gain and minimizing predation risk) and often compromise one or both objectives to achieve maximum gain under varying conditions (Sih, 1980).

Individuals' perception of risk may be affected by directly detecting predators (Dill and Fraser, 1984; Kieffer, 1991), the proximity to or amount of cover (Valone and Lima, 1987; Dill and Houtman, 1989; Bowers and Ellis, 1993), and by hearing alarm calls. While the presence of predators and cover in foraging behavior have been relatively well studied, this is not the case with alarm calls. Many species make use of alarm calls to signal potential danger (Dunford, 1970; Lishak, 1984; Blumstein, 1995; Blumstein and Arnold, 1995; Weary and Kramer, 1995; Hoogland, 1996; Blumstein and Armitage, 1997), and hearing these calls is assumed to increase an individual's perception of risk (Weary and Kramer, 1995) and can increase the probability of early detection of a predator (Hauser and Wrangham, 1990). In

response to alarm calls animals may assume an alert posture (Weary and Kramer, 1995), become more vigilant (Carey and Moore, 1986; Shriner, 1998), or flee into a refuge (Weary and Kramer, 1995; Shriner, 1998). Interestingly, although alarm calls are assumed to increase an individual's perception of risk, studies have generally looked at immediate responses to alarm calls such as increased vigilance. Rarely have studies tested whether hearing an alarm call affected other aspects of an individual's behavior, such as foraging, as we would predict if alarm calls do indeed increase an individual's perception of risk. If alarm calls do increase an individual's perception of risk, then we would expect increased alert and fleeing behavior in response to alarm calls just as we see with increasing distance to cover and the presence of model predators (Valone and Lima, 1987; Kieffer, 1991). In this study I examined the effects of conspecific alarm calls on the foraging behavior of Eastern chipmunks (*Tamias striatus*).

Eastern chipmunks are small, solitary, diurnal, terrestrial rodents (Kramer and Nowell, 1980; Giraldeau and Kramer, 1982; Clarke et al., 1993; Giraldeau et al., 1994; Otter, 1994; Bowers, 1995). They are often found in deciduous woods in habitats with high overstory and ground cover (Bowers, 1995; Brown and Morgan, 1995). Chipmunks have small (usually less than 0.5 ha), but widely overlapping home ranges (Dunford, 1970; Wood, 1993; Giraldeau et al., 1994). They are central place foragers, and center their activity around their burrow system (Kramer and Weary, 1991; Clarke et al., 1993) of underground runways in which they forage, cache, and defend food from conspecifics (Dunford, 1970; Wood, 1993).

Chipmunks are excellent subjects for studying the effects of alarm calls on foraging behavior. They are abundant, readily habituate to humans (Kramer and Nowell, 1980) and

exhibit virtually insatiable hoarding behavior (Kramer and Nowell, 1980; Kramer and Weary, 1991). Chipmunks give alarm calls in response to conspecifics, humans and other large animals (Dunford, 1970). An individual hearing these calls often assumes an upright or crouched alert posture, characterized by a lack of movement, and may flee the area (Dunford, 1970; Weary and Kramer, 1995). Thus, these behavioral changes suggest that hearing an alarm call does increase a chipmunk's perception of risk. In this study I will examine if chipmunks modify their foraging behavior in response to alarm calls. Specifically, I will investigate changes in the amount of food taken, time spent at the feeding station, and the degree of vigilance.

Methods:

This study was conducted in and around residential areas of Charleston, IL, USA, with study sites averaging approximately 0.75 ha in size and temperatures ranging from 18° C to 34 ° C over a 6 month period. Most contained grass lawns surrounded by woods and brush, creating an edge habitat through which chipmunks readily traveled.

Subjects were caught at the study sites from late-May through June 1998 using Sherman live traps baited with sunflower seeds; captured individuals were aged, sexed, and measured for body length to the nearest tenth of a cm using a tape measure. I marked each individual with varying spot patterns on the shoulder, midsection, and rump using different combinations of blond and black Clairol Nice 'N' Easy® hair dye applied with a paintbrush. Metal numbered eartags with plastic colored discs were also applied as a second measure of identification. Individuals were released immediately after handling and observations were

made to identify frequently used burrow entrances, home ranges, and common pathways of travel.

Feeding stations were constructed from a 20cm x 20cm x 2cm piece of wood with a plastic petri dish nailed to the center. These were set out for each individual approximately 5m from the central burrow so that chipmunks would find the feeding stations quickly (Bowers and Ellis, 1993). To habituate individuals to the feeding stations, I supplied striped sunflower seed for one month prior to experiments. Three different "playback" treatments were used; alarm call, control sound (white noise), and silent. I recorded alarm calls using a Marantz Model PMD222 portable cassette recorder, a Sennheiser System K6 microphone, and parabolic reflector. Chipmunks do not distinguish among individual callers (Weary and Kramer, 1995). Still, to control for chance recognition of a specific call, I obtained calls from multiple individuals from areas at least 1 mile from the study sites to create a set of exemplars for the playback trials. Using Canary Software (Charif et al., 1995), I eliminated background noise and selected three of the best series of notes; each series was spliced with itself to produce an exemplar. The rate of calls in a call series mimicked natural bouts of calls. These call series were then transferred back to a cassette tape in 20s bouts for playback; a similar method was used to create control sounds of white noise (Weary and Kramer, 1995; Mateo, 1996). All playbacks were broadcast from a Marantz portable cassette recorder through a single Advent Powered Partners AV570 speaker, powered by a Bescor PRO 10 Amp battery pack model PRB-10. The sound level of the playback was calibrated using a Radio Shack sound level meter to mimic the volume of chipmunk vocalizations heard in nature (Weary and Kramer, 1995). The speaker was housed in a wooden box with a

camoflauge cover; the speaker and observer were hidden approximately 3-4m from the feeding station.

Trials were conducted July through November between 0900 and 1700 CDT. During this study period natural chipmunk alarm calls were frequently heard at the study sites, but not during playback trials. Feeding stations contained 60 sunflower seeds (Kramer and Nowell, 1980; Bowers and Ellis, 1993), of known weight. All trials were videotaped with a HI 8 Canon camcorder, model ES3000, mounted on a tripod.

Each subject received all three treatments. All three treatments were given to an individual on the same day; at least 1/2h ($X \pm SE$: 42.6 ± 1.5 min) between control and alarm call playbacks for each individual was allowed to increase the likelihood of independence of treatments. Prior to a trial a subject had two undisturbed trips to the feeding station. The order of the treatments for an individual (silent, control, alarm call) as well as the particular exemplar call series was chosen at random for each trial. I first recorded whether travel to the dish was direct, with no stops, or delayed, in which the individual stops and scans (McAdam and Kramer, 1998). Just before the subject began to eat, I played a recording (either control sound or alarm call) for 20s; for silent trials, no recording was played. For the time that an individual was at a feeding station I recorded residence time (total time spent at the feeding station; Otter, 1994) and handling time (time spent loading, chewing, or manipulating food items). In addition, I recorded the frequency and duration of vigilant behavior: vigilant behavior included looking up, alert postures, and scanning (Otter, 1994; Weary and Kramer, 1995). The distance an individual ran to cover after collecting seeds, whether its travel away from the dish was direct or delayed, and its recovery time (the time from which the subject left the station until the time it re-emerged and was observed moving

toward the feeding station) were recorded as general response behaviors. To determine load size the remaining seeds were removed from the feeding station to be counted and weighed using a CT series Ohaus portable advanced electronic balance. This constituted the end of a single trial.

I used Cochran's Q test to conduct frequency comparisons of within-individual changes in behaviors for different treatments (Zar, 1996); Wilcoxon Signed Rank tests were used for within-individual comparisons of means. Statistical tests were nonparametric and corrected for ties where appropriate. Means are reported as $\pm$ SE. For simplicity, I present only the results of call versus control sound comparisons. No significant differences existed between silent and control treatments, and Friedman's nonparametric ANOVA tests incorporating all 3 treatments yielded results consistent with those presented below.

Results:

Ten out of twelve subjects responded with vigilant behavior to call treatments and did not respond to control treatments; of the other two subjects one responded to both the control and call sound and one did not respond to either playback treatment (Cochran's Q test: Q=10; P=0.0021). Chipmunks exhibited a greater degree of vigilant behavior with the alarm treatment than they did with the control treatment as shown by the higher frequency of look-up events and the trend towards more alert postures (Table 1). Thus, they spent a greater proportion of time vigilant throughout an entire trial after hearing an alarm call (Table 1). Interestingly however, although they responded to alarm calls, total residence time was greater for individuals following an alarm call treatments than for the control (Fig.1; $X_{control}$=60.5$\pm$ 5.9s, X_{call}=108.1$\pm$ 20.8s; Wilcoxon N=12; T=13; P=0.05).

Foraging behavior was also affected by alarm calls. Chipmunks took significantly fewer seeds after hearing an alarm call as opposed to a control sound ($X_{control}$=36.1±3.7 seeds, X_{call}=30.8± 4.1 seeds; Wilcoxon N=12; T=13; P<0.05), and exhibited a borderline trend towards taking lighter loads after hearing an alarm call ($X_{control}$=3.8± 0.3 g, X_{call}= 3.3± 1.2 g; T=14; P=0.0625). The lowered load size was not due to a decrease in the time spent handling food ($X_{control}$=42.3± 5.9s, X_{call}=64.2± 13.4s; Wilcoxon N=12; T=24; P=0.3125); rather, individuals loaded food items at a slower rate after hearing an alarm call (Fig. 2; $X_{control}$=0.1± 0.1 seeds/s loading, X_{call}=0.7± 0.1 seeds/s loading; Wilcoxon N=12; T=11; P=0.035).

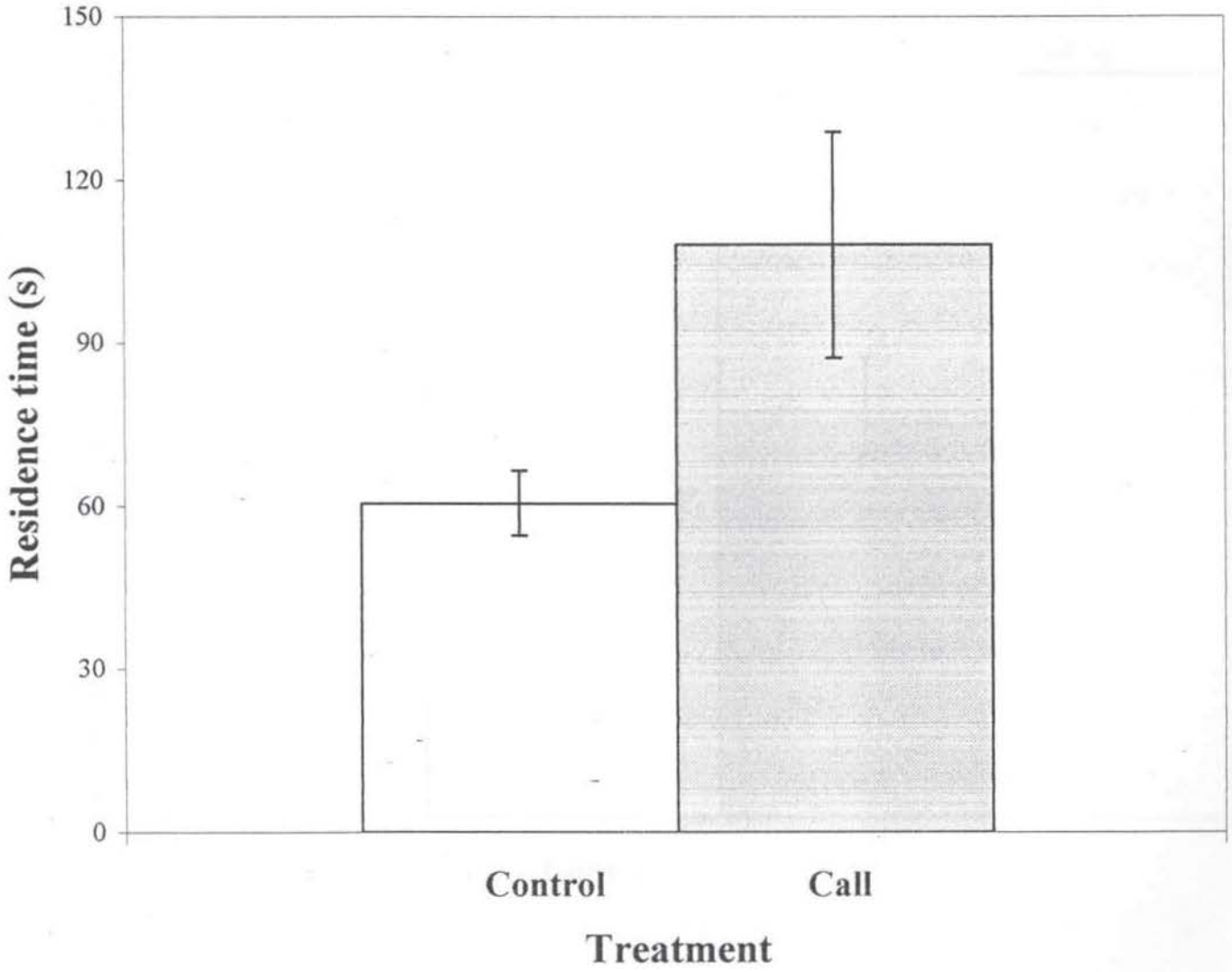
Chipmunks ran a shorter distance to cover with the alarm treatments than with the control after leaving the feeding station (Table 1). Individuals took significantly longer to re-emerge from the burrow and resume normal activity after the call treatments than after control treatments (Table 1). All 12 individuals exhibited a delayed approach to the feeding station regardless of the treatment. However, travel back to the burrow differed among treatments. Of the four individuals who exhibited differential travel between the control and alarm call treatments, all traveled directly back to the burrow after hearing an alarm call and delayed their travel back to the burrow after hearing the control sound (Cochran's Q: Q=5.993; P=0.05). Thus, chipmunks continued to respond calls with changes in their travel behavior after the alarm call.

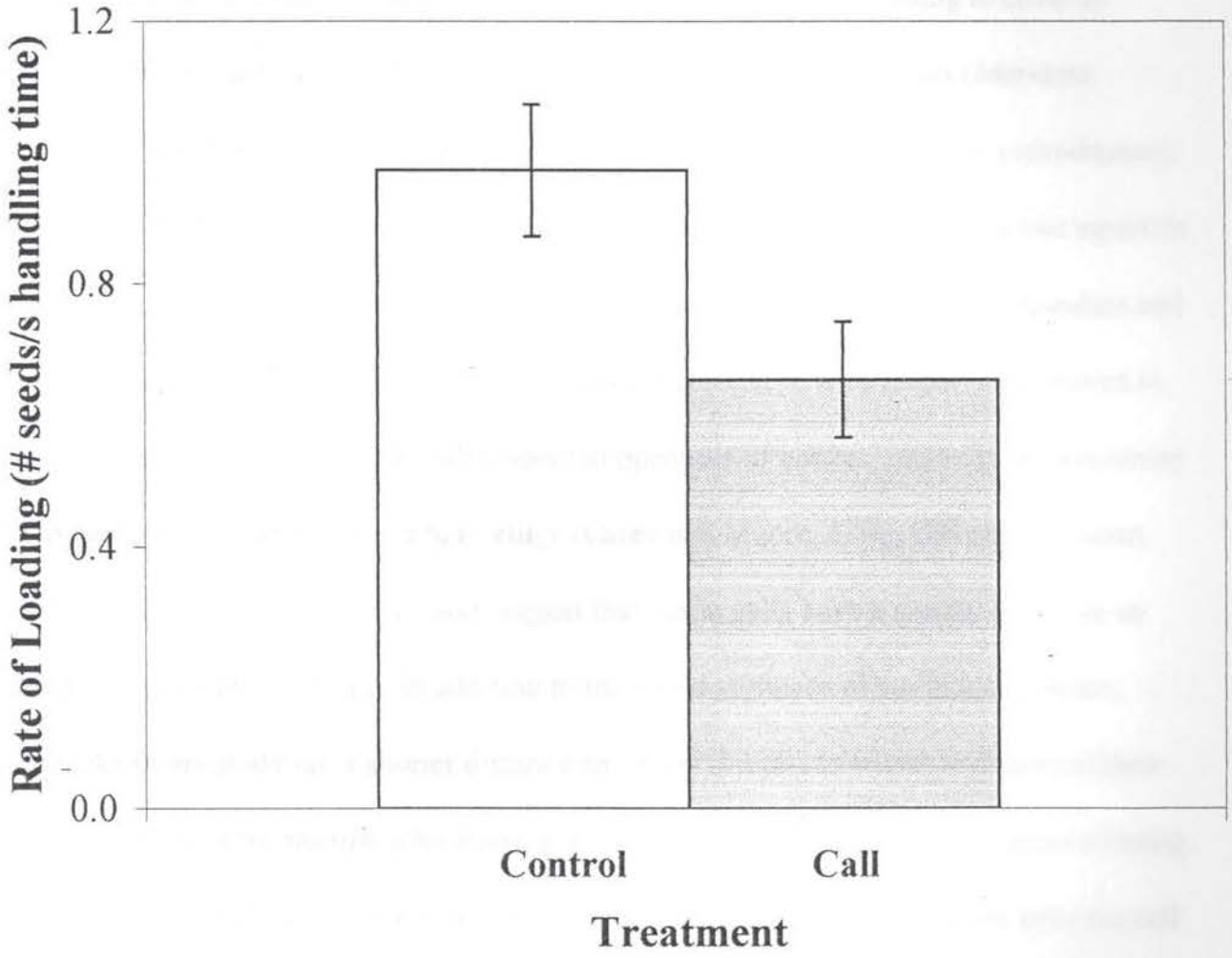
Table 1. Results of Wilcoxon signed rank tests for responses to control and alarm call treatments by Eastern chipmunks at feeding stations (N=12 individuals).

	Mean ± SE				
	Control	Call	df	Wilcoxon T	P
Number of Look-ups	12.0±1.5	15.4± 2.1	11	13	0.050
Number of Alert Postures	0.3± 0.1	0.9± 0.4	5	2	0.100
Proportion vigilance time	0.3±0.1	0.4±0.1	11	5	0.005
Recovery time (s)	143.9± 17.1	339.5± 65.1	11	1	0.001
Distance to cover (m)	3.9± 0.4	2.8± 1.0	11	2.5	0.003

Fig. 1. Residence time for Eastern chipmunks exposed to control and alarm call treatments at feeding stations. Error bars indicate $\pm$ 1 SE.

Fig. 2. Number of seeds collected per second handling time by Eastern chipmunks exposed to control and call treatments. Error bars indicate $\pm$ 1 SE.


150
120
90
60
30
0
Residence time (s)
Control
Call
Treatment


1.2
0.8
0.4
0.0
Rate of Loading (# seeds/s handling time)
Control
Call
Treatment

Discussion:

In this study I found that Eastern chipmunks generally react to and alter their foraging behavior in response to conspecific alarm calls. Their reactions to the alarm call were shown by the greater degree and duration of vigilance behavior exhibited while foraging at the feeding station when exposed to alarm calls. Such reactions to alarm calls have been found in a wide variety of sciurids. For example, increased vigilance and running to cover in response to alarm calls have been demonstrated in yellow-bellied marmots (*Marmota flaviventris*), golden-mantled ground (*Spermophilus lateralis*), Columbian (*S. columbianus*) and Californian (*S. beecheyi*), and Belding's ground squirrels (*S. beldingi*), and tree squirrels (Leger et al., 1979; Harris et al., 1983; Carey and Moore, 1986; Mateo, 1996; Blumstein and Armitage, 1997). These responses to alarm calls are consistent with responses observed in studies that varied predation risk with respect to openness of habitat, presence and proximity of a model predator, and distance to a refuge (Carey and Moore, 1986; Dill and Houtman, 1989; Kieffer, 1991; Otter, 1994), and suggest that alarm calls have a similar effect on an individual's perception of risk. In addition to increased vigilance at the feeding station, chipmunks in my study ran a shorter distance and more directly to cover, and delayed their re-emergence from the burrow after hearing an alarm call. These behaviors suggest a lasting effect of the call and that their perception of risk continued for several minutes after the call had stopped.

Brown (1988) predicted smaller load sizes with higher predation risk. In this study, chipmunks decreased their load size (number of seeds taken per trip) after hearing an alarm call. Other studies found similar shifts in load size after increasing predation risk by manipulating openness of habitat or proximity of a model predator (Brown, 1988; Kieffer,

1991; Bowers and Ellis, 1993; Bowers et al., 1993; Otter, 1994; but see Giraldeau and Kramer, 1982; Giraldeau et al., 1994). Since residence time was actually greater with the alarm call treatments than with the control, individuals were not simply decreasing the number of seeds by reducing the total time spent at the feeding station. This result is consistent with the idea that chipmunks adjust load size rather than foraging time when determining when to quit eating (Bowers et al., 1993). Unlike some animals such as grey squirrels (*Sciurus carolinensis*), chipmunks cease eating when they are vigilant (Otter, 1994; personal observation). Therefore, any time they spend on being vigilant is time they are not foraging. Furthermore, this study showed that whereas individuals did not alter the total amount of time they spent feeding, their loading was slowed after hearing an alarm call. This strongly suggests that by increasing vigilance after hearing an alarm call, chipmunks were sacrificing energy gain to reduce their chances of being attacked. To my knowledge, this is the first study to find a decrease load size in response to alarm calls and provides further evidence that alarm calls alter the perception of risk.

We would expect that animals would have shorter residence times with greater risk of predation (Holmes, 1984; Newman et al., 1988; Cowlishaw, 1997). However, one of the more interesting findings of this study was that chipmunks spent more time at the feeding stations after hearing an alarm call. Otter (1994) also found residence time for eastern chipmunks to be greater in open and presumably more risky habitats due to an increase in the frequency of vigilance events. This increase in residence time after hearing an alarm call may have been the result of the feeding stations being placed relatively close to the burrow in order to decrease the possibility of an intruding chipmunk visiting the feeding station and interfering with trials. Chipmunks may forage up to 150 m from their burrows (Kramer and

Nowell, 1980), but at close distances, familiarity with the area around the burrow may give individuals an advantage in predator avoidance through rapid recognition of predation risk, knowledge of refuges, and lower activity levels (Clarke et al., 1993). Chipmunks do not discriminate among sites according to microhabitat when they are close to their burrows but do so at greater distances from their burrows, suggesting that they respond highly to their distance from their burrows (Bowers, 1995). Whether chipmunks changed their foraging behavior in response to manipulation of cover and predators depended on their distance from the burrow (Bower and Ellis, 1993; Otter, 1994). Predation risk may therefore increase with distance to the burrow resulting in more risk-sensitive behavior farther away from the burrow (Bowers, 1995). Chipmunks may spend equal or less time at the feeding stations after hearing an alarm call if they are farther from their central burrow entrances in less familiar territory.

Another, non-exclusive explanation for greater residence time after hearing an alarm call concerns an individual's direct assessment of its risk of predation. While foraging, an individual may be able to assess the indirect components of its risk by means such as distance from its refuge, amount of cover in the habitat, and alarm calls (Lima and Dill, 1990; Weary and Kramer, 1995). In this study, individuals did not simply flee for a refuge after hearing an alarm call; rather, they became more vigilant. This suggests that, after hearing an alarm call, an individual directly assesses its own risk (e.g. looks for supporting evidence of a predator) rather than relying on others. To flee in response to the perceived risk of others without direct assessment of one's own risk may impose unnecessary temporal and energetic costs, resulting in a severe reduction in net energy gain (Burger et al., 1991). By becoming more alert and assuming a motionless posture, chipmunks can increase their

awareness of visual and auditory stimuli (Weary and Kramer, 1995), and may benefit from remaining at the feeding station for a longer time if they are able to assess their environment more effectively before returning to the burrow. How animals process information about their environment and convert it into an estimation of risk is unknown (Lima, 1998). We might, however, expect an interaction between the amount of individual assessment and distance from the burrow; individuals may adopt a more conservative foraging strategy by responding to external cues (e.g. alarm calls) at greater distances from the burrow.

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